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Comparing the morphology of *Potamogeton perfoliatus* L. along environmental gradients in Lake Balaton (Hungary)

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Abstract – *Potamogeton perfoliatus* readily adopts different morphological forms, and is therefore especially suitable for investigating variations of aquatic plants' morphology according to different environmental conditions. This paper discusses the morphological diversity of *P. perfoliatus* at different sites in Lake Balaton, where it occurs as one of the dominant species. We measured 11 morphological variables which were analyzed statistically within the environmental gradients present in the Lake (gradients in trophic condition, water depth and in wave exposure). We found morphological differences between the plants growing on the southern shallow shore which is more exposed to waves and those growing on the northern, deeper and sheltered shore as well as differences along the trophic and the water depth gradient. On the northern shore plants were significantly longer, their internodes were longer and their leaves were relatively thinner (greater Standard Leaf Area). Plants were larger in the more nutrient rich western basins of the Lake and also showed morphological changes along the water depth gradient. The different degrees of wave exposure probably interact partly with trophic differences due to lake morphology. However, we proved that modifications in plant morphology, of which some might be adaptive and therefore of importance in a changing environment, do occur in the common, submerged macrophyte *P. perfoliatus* in Lake Balaton.

Key words: Morphology / Lake Balaton / water depth / wave exposure / trophic gradient

Introduction

The ability to adapt to different environmental conditions is a basic trait of all plants, which ensures survival under changing conditions and serves as basis for the survival of the fittest. Aquatic macrophytes are exposed to a number of environmental gradients, which vary not only within their distribution range, but even within one lake (Hutchinson, 1975; Wetzel, 1975; Spence, 1982; Santamaria, 2002). Variations in certain traits might be generally interpreted as being adaptive if facts indicate that the achieved state is beneficial for the organism. Adaptation can occur in the plant's physiology – like the adaptation of the photosynthetic rate to light climate and has been researched for macrophytes thoroughly (Felföldy, 1960; Barko and Smart, 1981; Boston *et al.*, 1989; Tóth and Herodek, 2002; Tóth and Herodek, 2008). Modifications in life history which might be thought of as adaptive have also been shown (Van Wijk, 1988; Wiegleb and Brux, 1991; Barrett *et al.*, 1993). Changes in morphology due to changing or differing environmental conditions have been also reported by several authors, however most of them were mainly referring to growth, in terms of plant biomass, but some paid also attention to differences in plant architecture or in leaf shape (Pearsall and Hanby, 1925; Aiken, 1981; Barko and Smart, 1981; Idestam-Almquist and Kautsky, 1995).

The genus *Potamogeton* is especially apt in adopting different morphological forms in reaction to the environment (Casper and Krausch, 1980; Herr and Wiegleb, 1989; Preston, 1995; Kaplan, 2002). This is also true for *Potamogeton perfoliatus* L. as has been recognized already early (Glück, 1924) and first experimental attempts had been made as early as 1925 to connect morphology (leaf shape) with certain chemical conditions (Pearsall and Hanby, 1925). Hutchinson (1975) emphasizes the morphological variations that occur in *P. perfoliatus* (and some other species) triggered by differing environments and Kaplan (2002) described several interesting cases of phenotypic plasticity in different *Potamogeton* species. A relationship between morphological traits and environment can be regarded from two sides, and thereby

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knowing the morphological variations of a certain species makes it possible to use them as environmental indicators, as has been proposed (Aiken, 1981).

The ability to adapt is especially important under rapidly changing conditions (in one place, for a population) or in different environmental conditions as might occur across a broad geographic range, inhabited by a widely distributed species (such as most aquatic species are, *e.g. P. perfoliatus* all the temperate regions except North America).

Lake Balaton is large (597 km^2), shallow (mean depth: 3.3 m) and of elongate shape. Its north-western shore is rather protected, has a constant, rather steep depth gradient, its sediments are silty and more nutrient-rich whereas the south-eastern shore (hereafter called "northern" and "southern" shore, respectively, for sake of simplicity) is more wave exposed, with a sandbar all along the shore creating a shallow water zone (0.5–1 m) of larger grained sediment (Entz and Sebestyén, 1942; Máté, 1987; Zlinszky *et al*., 2008). Prevailing north-north-eastern winds (Tóth, 1960; Istvánovics *et al*., 2008) are the underlying cause for several differences in shore characteristics, as they entail the accumulation of finer textured sediments on the northern site and the deposition of bigger particles on the southern shore (Máté, 1987). Finer grained sediments are generally more nutrient rich, and support better macrophyte growth (Barko and Smart, 1986). Apart from this striking north-south difference, there is a west-east gradient due to the only big inflow to the lake at the westernmost point, the River Zala, which constitutes the major external nutrient source. Hence, there is a trophic gradient from west to east, reaching nowadays from eutrophic in the westernmost basin to mesotrophic in the eastern basin (Présing *et al*., 2007).

P. perfoliatus is one of the dominant species in Lake Balaton, occurring all around the lake, next to *Myriophyllum spicatum*, intermingled with *Potamogeton pectinatus* at the shallower sites. Macrophyte occurrence in the shallow and turbid Lake Balaton is limited to a very small area, which can be mainly attributed to light deficiency. Only 1.1% of the total lake area were found macrophyte covered in the single whole lake macrophyte mapping in 1978 (Juhász, 1981), and plants grew until 1.5–2.5 m depth on the northern shore and to 0.5–1 m on the southern shore. Similar distributional limits were observed in a survey in 2006, where submerged plants grew on average no deeper than 2.6 m on the northern shore and 1.3 m at the southern shore (Istvánovics *et al*., 2008). Distribution is mainly confined by light deficiency in the highly turbid lake, however, wave action also contributes to limiting distribution, especially on the southern shore, as Istvánovics *et al*. (2008) have concluded.

Istvánovics *et al*. (2008) have attempted to define the factors controlling the occurrence of macrophytes on the different shores of Lake Balaton. However, absence (or presence) is just one, radical answer to habitat conditions, but there is a whole range of possible reactions to environmental conditions which are the before mentioned modifications in physiology, life-history or morphology. As none of these have been examined before, as a first step we decided to investigate the latter for one of the main macrophyte species in Lake Balaton, for *P. perfoliatus*. Regarding the great variability of *P. perfoliatus*, it is to be expected that it will show changes in its morphology to environmental factors, in the present case to the very much differing conditions at sites around the lake, constituting therefore a suitable model for examining how macrophytes react to environmental changes. The objective of this study was to investigate to what extent the observed morphological variability can be related to environmental factors. Assuming simple reactions on the one hand and possibly adaptive changes on the other hand, the following hypotheses were formulated:

1. Nutrient richer sites: size dependent traits (like shoot length, total biomass) should be larger.
2. Increasing water depth: length (of shoot and internodes) and therefore biomass, leaf area, and SLA should increase (more light intercepting surfaces for compensation of less light in greater depths and also smaller but tougher leaves in shallower and therefore more wave-exposed sites).
3. Wave exposed shore: plants with tougher appearance (greater stem density, relatively thicker leaves with smaller area but more elongate).

For testing these hypotheses, differences in the species' morphology were analyzed together with abiotic factors such as trophic state, wave exposure and water depth.

Material and methods

Sampling sites

As Lake Balaton exhibits differing conditions in basically two more or less orthogonal directions – a trophic gradient from west to east and two main exposure types represented by the southern/northern shore – sampling sites were chosen in order to reflect these differences: about half (8 and 9) were on the southern and on the northern shore, respectively.

As phosphorus content of the sediment as well as of the water declines steadily from west to east and thereby creates a trophic gradient, sampling sites chosen randomly from among all vegetated and accessible points along the two main shores were aligned along this gradient. Data of the chemical properties of the sediment was obtained from the map server of the University of Keszthely (http://vektor.georgikon.hu/website/meder/viewer.htm) and from Csermák and Máté (2004) and is shown in Table 1.

Wave exposure is mainly determined by winds coming from the prevailing wind direction – which is north-western at Lake Balaton – and the fetch length. Fetch lengths for our sampling sites on the southern shore were more than 20-fold bigger (up to 9.5 km) than fetch lengths for northern shore sampling sites, where it was 240 m on average.

Table 1. Sampling sites with sampled water depths, geographic fetch length (fetch), and distance from western shore (distW), shore (N – northern, S – southern) and chemical characteristitcs (P: P_2O_5, N: total N, $CaCO_3$ and pH).

Site	Samples from water depth in June	July	August	Fetch [m]	distW [km]	Shore	P [mg.kg^{-1}]	N [%]	$CaCO_3$ [%]	pH
A	60	70	60	414	0	S	282.50	1.88	34.20	7.77
B	70, 90, 110	55, 70, 95	50, 70	7808	3	S	265.50	0.93	27.40	7.10
C	35, 70, 90	15, 50, 75	50, 70	6183	10	S	201.50	0.25	41.85	7.25
D	65, 80	50, 85	80	8169	12	S	152.00	0.20	39.80	7.49
E	100	60, 80	55, 70	6110	24	S	164.00	0.19	42.50	7.52
F	-	95	85	7521	51	S	68.00	0.06	24.00	7.54
G	80	75	55, 85	9546	56	S	28.50	0.05	24.50	7.89
H	75, 100, 110	60, 85	50, 70	8633	59	S	71.00	0.05	16.00	7.27
I	140	130	100	1032	6	N	191.00	1.76	53.40	7.70
J	210	190	180	67	8	N	217.00	0.23	53.80	7.44
K	135	115	110	474	15	N	163.50	0.28	53.85	7.18
L	140	140	130	278	19	N	199.00	0.13	59.00	7.62
M	240	170	160	156	28	N	143.00	0.09	49.20	7.38
N	110, 140	85, 100, 125	125	337	41	N	79.50	0.20	52.00	7.05
O	160, 190	150, 160	150, 170	240	53	N	99.00	0.23	37.00	7.22
P	140, 220	220	190	172	58	N	112.00	0.22	59.00	7.40
Q	70, 110, 140	90, 110, 140	85, 100, 120	154	65	N	216.50	0.21	48.00	7.05

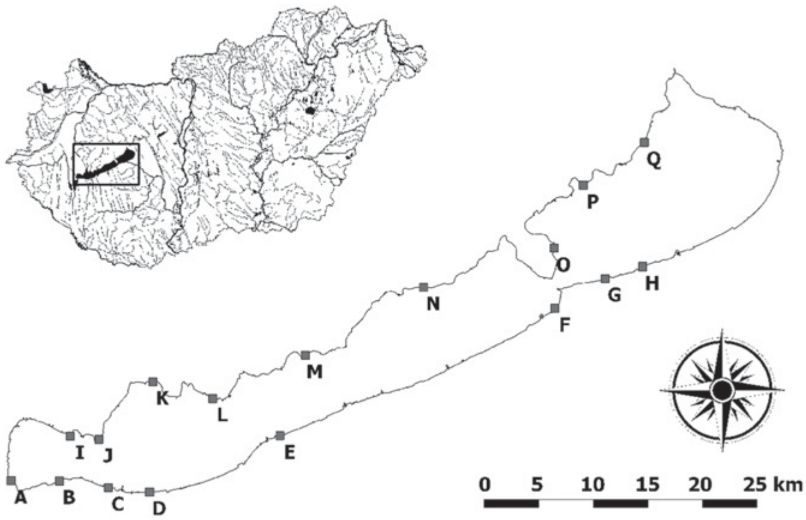

Fig. 1. Lake Balaton within Hungary and sampling sites (squares) around the lake.

As Lake Balaton is highly turbid, its water exhibits high values of extinction (mean vertical light attenuation coefficient K_d about 1.9 m^{-1}). Therefore, if we regard the light that reaches plants growing from the bottom of the lake, we can assume a rather steep light gradient with declining light values as water depth increases.

Sampling

During summer 2007, 17 sampling points around the lake (Fig. 1), distributed on both shores were visited monthly, *i.e*. in June, July and August. Each time, 5 (4–6) shoots were collected on average at each sampling site chosen randomly from within the detected vegetated spots. As vegetation in Lake Balaton is generally not continuous, sampling at the different sites orthogonally to the shore, along a water depth gradient could not always be executed, but where vegetation occurred at different depths on one site, 5 samples were taken from each depth within the one site (see Tables 2–4 for exact number of replicates (*n*) and Table 1 for water depths).

Measurements

By choosing parameters reflecting features of the whole plant as well as others referring to shape and size of leaves we tried to cover the whole range of possible morphological variations. The following 11 parameters were chosen or calculated: shoot length (length of whole shoot from stem base till tip of furthest leaves), internode

Table 2. Means of morphological features measured on *Potamogeton perfoliatus* at sampling sites along the shores of Lake Balaton in June. Water depths 1–3 as given in Table 1.

	South						
June	West A	B	C →	D →	E →	G	East H
n (depth 1)	4	5	5	4	4	5	5
n (depth 2)		4	4	4			6
n (depth 3)		4	5				6
Shoot length [cm]	79.6	96.8	62.2	83.8	58.6	32.0	27.5
Internode length [cm]	2.3	2.3	2.0	3.2	2.1	1.4	1.3
Leaf area [cm^2]	5.4	7.4	4.8	9.8	5.1	4.2	4.6
Leaf length:width	2.2	1.8	1.8	1.6	2.0	1.4	1.5
SLA [$cm^2.g^{-1}$]	368	399	423	408	397	410	409
Number of leaves	33.8	34.7	27.6	25.5	28.0	25.2	21.8
Stem diameter [cm]	0.31	0.30	0.30	0.36	0.30	0.33	0.30
Stem density [$g.cm^{-3}$]	0.07	0.07	0.09	0.15	0.07	0.08	0.06
Stem DW [g]	0.26	0.39	0.22	0.41	0.22	0.11	0.12
Leaf DW [g]	0.51	0.58	0.31	0.58	0.36	0.26	0.24
Total DW [g]	0.78	1.26	0.68	1.41	0.59	0.37	0.37

	North								
	West I	J	K →	L →	M →	N →	O →	P	East Q
n (depth 1)	4	3	4	4	4	5	5	4	4
n (depth 2)						4	5	3	4
n (depth 3)									4
Shoot length [cm]	31.4	134.7	74.6	78.3	112.9	51.1	76.2	83.9	57.2
Internode length [cm]	3.5	9.0	3.2	4.3	3.4	2.4	3.4	4.0	2.3
Leaf area [cm^2]	10.3	13.5	9.6	9.6	9.6	3.9	7.4	5.0	5.1
Leaf length:width	2.1	2.5	2.0	2.3	2.0	1.8	1.5	2.0	1.6
SLA [$cm^2.g^{-1}$]	497	325	486	552	469	564	477	471	457
Number of leaves	8.5	13.7	25.0	14.8	31.0	21.8	20.4	21.4	23.9
Stem diameter [cm]	0.37	0.35	0.38	0.38	0.33	0.22	0.33	0.25	0.32
Stem density [$g.cm^{-3}$]	0.13	0.11	0.12	0.14	0.08	0.03	0.08	0.03	0.08
Stem DW [g]	0.12	0.42	0.27	0.32	0.39	0.14	0.24	0.19	0.23
Leaf DW [g]	0.15	0.52	0.45	0.28	0.60	0.15	0.31	0.22	0.27
Total DW [g]	0.28	0.94	0.73	0.61	0.99	0.29	0.54	0.41	0.52

length, mean leaf area (LA), leaf length:width ratio (L:W), standard leaf area (SLA = leaf area/leaf dry weight), number of leaves (on main branch), stem diameter at the base, stem mass density (stem dry weight/stem volume – latter approximated as a truncated cone for including the difference between stem base and stem tip diameter), stem dry weight (dry weight = DW, of main stem), leaf DW (totalled for all leaves on main stem), total plant DW (main stem + leaves on main stem + side branches). Shoot length and stem diameter were measured with measuring tape and calliper. Leaves were scanned and their dimensions acquired with the help of the software ImageJ (http://rsb.info.nih.gov/ij/) with the accuracy of 0.01 mm. Leaves and stems were dried at 105 °C and weighed. Traits referring to leaves were averaged for each plant.

Data analysis

Based on these parameters data was analyzed applying multivariate and bivariate statistics. A Principal Component Analysis was performed (with data standardized by its standard deviation), adding convex polygons afterwards to picture potential patterns, using the SynTax program package (Podani, 2000). Additionally, these 11 variables were tested with a General Linear Model (GLM) (using Statistica), consisting of the shore as categorical variable, water depth and phosphorus content as continuous variables, considering also interactions between categorical and continuous variables and applying a Bonferroni-correction to correct for multiplicity of *p*-values to $p < 0.004$. Normality of error and homogeneity of variance was checked visually on residual-Q-Q plots, graphs of residuals *versus* fitted values and histograms of residuals. Based on these, data was transformed as follows: for June internode length was square root transformed, stem density, stem DW and total DW were log-transformed; for July shoot length was square root transformed and internode length, LA, SLA, stem density, stem DW, leaf DW and total DW were log-transformed; for August stem DW, leaf DW, and total DW were square root transformed, shoot length, internode length, LA, SLA and stem density were log-transformed. Model choice took into account that the interaction between water depth and shore was never significant, thus it was omitted from the model.

Table 3. Means of morphological features measured on *Potamogeton perfoliatus* at sampling sites along the shores of Lake Balaton in July. Water depths 1–3 as given in Table 1.

	South							
	West →							East
July	A	B	C	D	E	F	G	H
n (depth 1)	4	4	4	4	4	5	4	3
n (depth 2)		4	4	4	4			8
n (depth 3)		4	4					
Shoot length [cm]	43.0	38.9	39.3	55.2	44.2	38.0	59.1	29.2
Internode length [cm]	1.5	2.0	1.7	2.1	1.6	1.7	2.0	1.1
Leaf area [cm^2]	6.2	6.3	4.9	7.6	4.1	4.1	4.6	3.8
Leaf length:width	2.0	1.7	1.8	1.7	1.7	1.6	1.3	1.6
SLA [cm^2.g^{-1}]	428	443	329	439	306	324	317	375
Number of leaves	20.8	18.8	18.8	26.5	22.9	21.0	28.5	25.5
Stem diameter [cm]	0.32	0.32	0.30	0.34	0.29	0.31	0.39	0.30
Stem density [g.cm^{-3}]	0.08	0.12	0.11	0.14	0.09	0.09	0.16	0.06
Stem DW [g]	0.19	0.18	0.16	0.34	0.16	0.18	0.32	0.12
Leaf DW [g]	0.28	0.23	0.28	0.48	0.32	0.26	0.42	0.31
Total DW [g]	0.54	0.47	0.87	0.93	0.76	0.44	1.08	0.43

	North								
	West →								East
	I	J	K	L	M	N	O	P	Q
n (depth 1)	4	4	5	4	4	4	4	4	4
n (depth 2)						4	4		5
n (depth 3)						4			4
Shoot length [cm]	23.7	176.8	15.5	108.8	71.5	38.8	87.9	68.2	68.8
Internode length [cm]	1.1	5.3	1.0	4.0	2.9	1.8	3.4	2.7	2.5
Leaf area [cm^2]	5.6	13.5	5.2	8.7	11.0	4.3	7.5	5.7	4.5
Leaf length:width	1.9	1.8	2.1	2.3	2.0	1.8	1.5	1.8	1.6
SLA [cm^2.g^{-1}]	539	283	643	538	530	502	419	524	444
Number of leaves	19.8	35.0	13.0	26.8	26.3	18.5	23.4	25.8	31.2
Stem diameter [cm]	0.29	0.44	0.23	0.34	0.36	0.24	0.33	0.34	0.29
Stem density [g.cm^{-3}]	0.05	0.39	0.02	0.08	0.09	0.04	0.10	0.06	0.05
Stem DW [g]	0.06	1.56	0.03	0.39	0.25	0.13	0.47	0.25	0.22
Leaf DW [g]	0.20	1.40	0.09	0.44	0.50	0.16	0.42	0.25	0.30
Total DW [g]	0.28	4.21	0.13	0.91	0.78	0.31	1.00	0.51	0.53

Results

In general, *Potamogeton perfoliatus* shoots from Lake Balaton were 54.8 cm long with internodes being 2.2 cm apart, and shoots bearing 23 leaves on average (min. 7, max. 52), which had a mean length of 3.7 cm and mean width of 2.1 cm, making a leaf length:width ratio of 1.8. Mean leaf area was 5.8 cm^2. The stem was 0.3 cm wide on average and the plant's total dry weight was about 0.6 g, with 0.3 g of total leaf DW (50% of total DW) and 0.2 g of stem DW (33% of total DW). Branches, which were originally measured too, but were due to their infrequency not included in the analyses, constituted the remaining 17%.

A survey of the resulting mean parameters at the different places from June till August is given in Tables 2–4.

Ordination results – whole lake overview

Principle Component Analysis for the three months showed that no distinct groups can be defined. Grouping samples by connecting them with convex polygons according to the shores (as to be seen in Fig. 2), we found that the polygons overlap to a great extent, or even include one in another. Plants from the northern shores were distributed over a bigger area of the plot, indicating more variable features. Looking at the different examined traits (Fig. 3), we found two groups. The "size"-group, consisting of mostly size-related traits like leaf dry weight, shoot length, stem dry weight and total dry weight, and another group made up of leaf area, stem diameter, stem density and internode length. These traits were interconnected at all three sampling times. The former ("size") group ran more or less parallel to the first PCA axis, explaining 47, 53 and 51% of total variance in the data for June, July and August, respectively, whereas the latter could be connected with the second PCA axis and an explained variance of 20 (15 and 16)% (Fig. 3). Standard leaf area (SLA), leaf length:width ratio and the number of leaves stood separated from these two groups and more or less opposite to them. Including the environmental variables "water depth" and "phosphorus content" as background variables in a joint plot (Fig. 4), the latter ran parallel to the first axis and the former parallel to the second axis

Table 4. Means of morphological features measured on *Potamogeton perfoliatus* at sampling sites along the shores of Lake Balaton in August. Water depths 1–3 as given in Table 1.

	South							
	West →							East
August	A	B	C	D	E	F	G	H
n (depth 1)	4	5	4	4	4	4	5	5
n (depth 2)		4	5		5		5	5
n (depth 3)								
Shoot length [cm]	22.6	26.1	47.0	24.5	36.2	23.2	17.0	30.4
Internode length [cm]	1.0	1.5	1.8	1.2	1.1	1.2	0.8	1.2
Leaf area [cm^2]	3.6	4.8	5.0	5.5	3.5	3.3	2.7	3.0
Leaf length:width	2.2	2.0	1.8	1.7	1.3	1.6	1.9	2.0
SLA [cm^2.g^{-1}]	269	356	321	412	348	433	365	364
Number of leaves	20.3	14.4	19.1	10.8	30.6	17.4	18.5	25.4
Stem diameter [cm]	0.33	0.31	0.36	0.37	0.33	0.28	0.24	0.28
Stem density [g.cm^{-3}]	0.10	0.09	0.12	0.19	0.08	0.06	0.04	0.05
Stem DW [g]	0.13	0.12	0.25	0.15	0.17	0.10	0.06	0.12
Leaf DW [g]	0.26	0.22	0.40	0.19	0.36	0.16	0.15	0.21
Total DW [g]	0.39	0.34	0.72	0.35	0.54	0.26	0.22	0.34

	North								
	West →								East
	I	J	K	L	M	N	O	P	Q
n (depth 1)	5	6	5	5	5	5	4	5	5
n (depth 2)							5		5
n (depth 3)									5
Shoot length [cm]	56.2	100.8	19.7	77.3	46.8	35.1	71.0	72.3	52.0
Internode length [cm]	1.7	3.5	0.9	3.3	4.4	1.8	3.2	3.3	1.8
Leaf area [cm^2]	7.2	6.9	2.2	8.6	12.3	3.7	8.0	6.1	4.2
Leaf length:width	2.0	1.9	2.2	2.3	2.0	1.7	1.5	2.1	1.7
SLA [cm^2.g^{-1}]	462	545	634	552	417	432	373	512	425
Number of leaves	29.0	28.3	19.8	20.4	12.2	15.8	20.0	21.4	26.1
Stem diameter [cm]	0.32	0.37	0.18	0.37	0.40	0.25	0.35	0.32	0.28
Stem density [g.cm^{-3}]	0.08	0.11	0.01	0.10	0.18	0.04	0.13	0.07	0.06
Stem DW [g]	0.26	0.55	0.02	0.30	0.19	0.14	0.34	0.27	0.24
Leaf DW [g]	0.44	0.41	0.07	0.36	0.31	0.15	0.39	0.26	0.29
Total DW [g]	0.71	0.99	0.09	0.69	0.51	0.29	0.83	0.65	0.54

at all three examination dates. That means that the size-related features were aligned with the phosphorus content gradient, whereas LA and stem parameters ran along the water depth.

Trophic gradient

Evaluating statistically significant differences (see Table 5) in plant morphology from the different sites, a gradient along the sites differing in phosphorus content could be detected (mainly in June, much less distinct in July and August), which was best seen in the group of traits reflecting the absolute size of the plants (including leaf dry weight, stem dry weight, plant length and total dry weight). Values of traits significantly affected by phosphorus content always proved to decline towards lower phosphorus values.

Northern-southern shore

Significant differences between the northern and the southern shores could be seen in several cases (number of leaves, SLA, stem diameter, stem density, leaf DW), especially clear in July (Table 5).

Plants were in few traits non-significantly larger on the northern shore (shoot length, leaf area), but were bigger or thicker in most of their features on the southern shore (smaller SLA – meaning relatively thicker leaves, stronger stems – greater diameter and stem density, greater total dry mass).

Water depth

According to our GLM analysis, several traits depended on water depth, including leaf area, stem density, stem diameter, internode length, leaf dry weight (only in July), stem dry weight, shoot length and total dry mass (Table 5). Traits on which water depth had a significant effect were always increasing towards deeper water.

Seasonality

A temporal trend could also be observed, comparing data from June till August: in June plants were higher

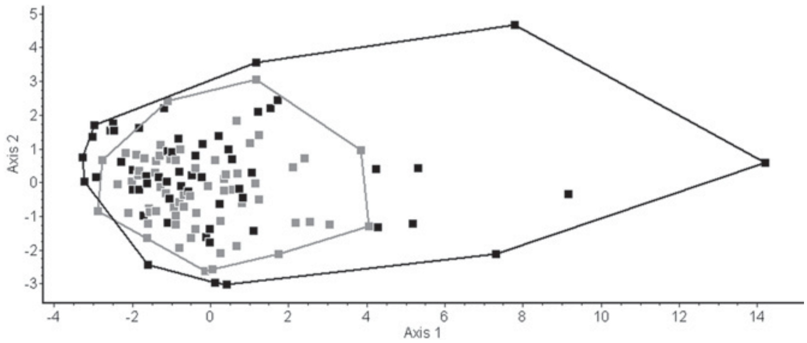

Fig. 2. PCA on morphological traits of *Potamogeton perfoliatus* shoots from July, showing northern shore (black squares with black line) and southern shore (grey squares with grey line) samples within convex polygons.

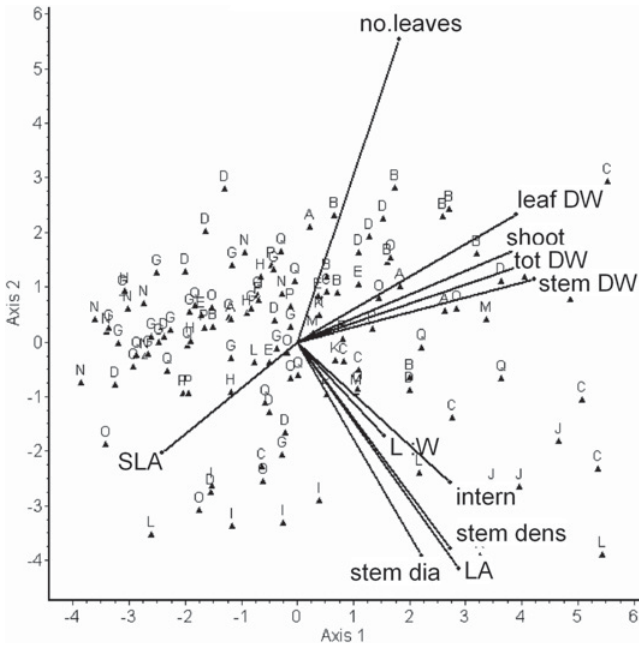

Fig. 3. PCA biplot of *Potamogeton perfoliatus* shoots according to morphological traits in June. Abbreviations clockwise: SLA: standard leaf area, no.leaves: number of leaves, leaf DW: leaf dry weight, shoot: shoot length, tot DW: total dry weight, stem DW: stem dry weight, L:W: leaf length:width ratio, intern: internode length, stem dens: stem density, stem dia: stem diameter, LA: leaf area. Triangles with letters: samples with letters for sampling sites as in Figure 1.

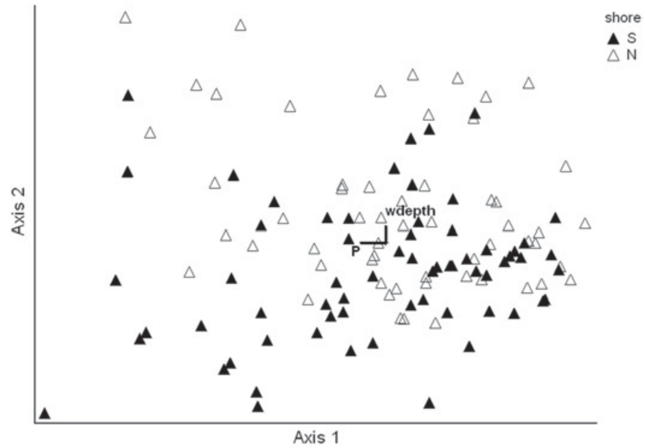

Fig. 4. Jointplot of *Potamogeton perfoliatus* shoots according to morphological traits from the northern (open triangles) and the southern shore (filled triangles) in June showing gradient in phosphorus content (P) and water depth (wdepth).

and heavier (dry weight) than in August (Tables 2–4). There were fewer significant differences in August than in the previous months (Table 5). In June the influence of the trophic gradient was the most obvious, but also some effects of the northern/southern shores (*e.g.* stem diameter) and few differences in line with the water depth gradient could be seen. In July differences along the two major shores became more evident, while those based on nutrient conditions became fewer and water depth showed the strongest impact on plant traits. In August only few significant effects could be observed, which were mainly related to water depth.

Discussion

Different environmental forces act on *P. perfoliatus*'s morphology in Lake Balaton of which we showed several to vary along these gradients. Differences were shown along a trophic gradient (which corresponds to the longitudinal axis of the lake), along a water depth gradient and between the two main shores.

Principal Component Analysis showed no distinct separation of any groups, but it did order plants from different sampling sites along the above mentioned gradients of trophic condition and water depth. Plants from the more sheltered (northern) shore appeared to be more variable, which is in line with the findings of Idestam-Almquist and Kautsky (1995), who proved experimentally that *Potamogeton pectinatus* plants originating from a sheltered site exhibit more variable features than specimens from an exposed site of the same area. They found that this pattern is genetically fixed at the population level. Translocation experiments would be one way to establish whether this is the case for *P. perfoliatus* in Lake Balaton, too.

Table 5. Significant effects on morphological differences between *Potamogeton perfoliatus* shoots at different sites in Lake Balaton in the researched three months. SLA: standard leaf area, DW: dry weight, S: Southern, N: Northern, P: phosphorus. Significant effects marked with * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

	S/N-shore			P content			Water depth			Shore × P		
Trait	June	July	August	June	July	August	June	July	August	June	July	August
Shoot length [cm]				**	**		***	***	**			
Internode length [cm]				**	*		***	***	***			
Leaf area [cm^2]				***	*		***	***	***			
Leaf length:width				***			**					
SLA [$cm^2.g^{-1}$]	N > S***	N > S**										
Number of leaves		S > N***									***	*
Stem diameter [cm]	S > N**	S > N**		**				***	**	***		
Stem density [$g.cm^{-3}$]	S > N***	S > N*		***				***	*	**		
Stem DW [g]		S > N*		***		*		***	**			
Leaf DW [g]		S > N***		***			*	***			*	
Total DW [g]		S > N**		***				***	*			

Our results were mainly significant in June and July, which can probably be attributed to a general declining tendency towards the end of the season in August with the onset of senescence. This is supported by the fact that absolute plant sizes were also decreasing. Seasonality might also have some confounding effect on plant size data, as the age of the harvested shoots is not known.

The inflowing Zala River provides the major nutrient charge in the westernmost end of Lake Balaton, the gradient in nutrient supply is equivalent to an east-west gradient, being high in the west and gradually decreasing to the east. We found several morphological traits reflecting the absolute size of the plants (total dry weight, shoot length, leaf and stem dry weight), to grow with increasing phosphorus values, as outlined in our hypotheses. This is remarkable if considering, that phosphorus levels were in all sites above the limiting level.

Changes in the depth of water in the researched ranges might have mainly two, rather contra-acting effects: one is the better light availability in shallower water, which is a general and significant process in the highly turbid waters of Lake Balaton as described in 'Sampling sites' and is therefore regarded here as possible explanatory factor without knowing any exact values, only the direction of the underlying mechanism. The other effect of low water depth is increased wave action, which occurs as waves break on the shallow lake bottom, and cause bed disturbance (Smith, 1979 in Spence, 1982), possibly breaking plant shoots and damaging plant tissue (Idestam-Almquist and Kautsky, 1995; Puijalon *et al*., 2005; Schutten *et al*., 2005). Observed morphological changes along the water depth gradient were probably mainly due to decreasing light intensity in deeper water and can be interpreted as attempts to compensate the disadvantages of shading (Maberly, 1993). Most of our results are in line with the proposed hypotheses (*e.g.* the increase in leaf area, in internode length or total dry weight), whereas some of the observed changes seem to contradict the notion of relatively less exposed deeper sites (higher stem mass density, stem diameter). Measurements by Pearsall and Pearsall (1923), Spence and Chrystall (1970) and Maberly (1993) support most of our results (internodes shorter and thicker leaves in shallower water; SLA and leaf dry weight greater in deeper water).

Differences between the two main shores result mainly from the prevailing wind direction, which is north-western, and causes the southern shore to be more wave exposed, accumulating larger particles in the sediment and thus holding less nutrients than the wind and wave protected northern shore with silty, more nutrient rich sediments (Entz and Sebestyén, 1942; Somlyódy and Koncsos, 1991; Istvánovics *et al*., 2008). Plants on the southern, exposed shore were as expected tougher, with smaller but relatively thicker (SLA) and slightly more elongate leaves (not significant), thicker, heavier and denser stems. These modifications might be regarded as being adaptive, as they are probably beneficial for the plant, offering on the one hand less surface for wave force to act upon and on the other hand building structures more resistant to mechanical stress, altogether making plants more durable to heavier wave exposure. Our findings are endorsed by the results of several authors who found adaptations in morphological features to mechanical stress, like Puijalon *et al*. (2005) on *Berula recta*, or Boeger and Poulson (2003) on submerged *Veronica anagallis-aquatica* plants, whereas others stated differences in morphology with a possibly adaptive value (Idestam-Almquist and Kautsky (1995) on *P. pectinatus*). Effects of reduced nutrient supply on the sandy, southern sediments, which have been described also for other species (Entz and Sebestyén, 1942; Aiken, 1981; Barko and Smart, 1986; Hangelbroek *et al*., 2003) are overlying, and strengthening the effects of mechanical stress, so that it remains the task of future, experimental research to unravel these two effects.

Our results show that morphological variability of the submerged macrophyte *Potamogeton perfoliatus* can be linked rather well to certain environmental gradients existing in Lake Balaton, such as trophic state, wave exposure and water depth. Some of the observed responses in morphology can certainly be interpreted as actually induced by environmental forces and furthermore also as being adaptive, whereas for the interpretation of some other features data needs to be tested experimentally.

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